Whitebark pine (*Pinus albicaulis* Engelm.) seed production in natural stands

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Abstract

The mature cones of whitebark pine from two high-elevation natural stands in central Idaho and western Nevada were analyzed in 2004 to determine the seed numbers and quality. It has the typical 2-year pine reproductive cycle. Cones are indehiscent and deciduous at maturity and the seeds lack seed wings. Cones averaged 62 scales, 75% of which were fertile with a seed potential of 96 seeds per cone. Total seeds per cone averaged 66 of which 46 were filled. Other potentially filled seeds were lost for different causes including abortion before pollination, abortion soon after pollination due to a lack of pollination or self-pollination, abortion about the time of fertilization due to self-fertilization, abortion during early and late-embryo development, and damage by insects or disease during development. About 70% of total seeds were filled and likely viable, which is high for conifers in natural stands especially at high elevations.
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1. Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) has an extensive but very scattered distribution at high elevations from 1000 m in coastal areas of British Columbia (B.C.), 1700–2200 m in the Cascade Mountains of Oregon and Washington up to 3600 m in the Sierra Nevada of northern California to 2200 m in elevation in the interior of B.C. and 1900–2300 m in western Alberta and from 1900 to 3300 m the Inland Empire forest regions of eastern Washington, Northern Idaho, western Montana and northwestern Wyoming (Critchfield and Little, 1966; Hosie, 1979; Farjon, 1998). The most accurate distribution map is given by Critchfield and Little (1966). It grows on thin soils near the upper tree line often on rocky faces and cliffs. Under such conditions it grows slowly and trees often have several tops and considerable top-damage due to wind and snow (Fig. 1). It seldom forms pure stands, however, it may on deep well-drained soils where it grows well (Hosie, 1979).

Whitebark pine is a five-needle white pine, belonging to the Subgenus Strobus, Section Strobus, Subsection Cembrae, the stone pines. Cones are indehiscent and deciduous at maturity (Fig. 2), and seeds lack wings (Little and Critchfield, 1969). Well-known related species are *P. siberica* Du Tour (Siberian stone pine) and *P. cembra* L. (Swiss stone pine) of Asia and Europe (Little and Critchfield, 1969; Farjon, 1998). Whitebark pine is the only stone pine native to North America, but there are several North American white pines.

White pines are susceptible to white pine blister rust (*Cronartium ribicola*), which lives part of its life cycle on *Ribes* shrubs. The fungal spores infect the pine needles and the fungal hyphae grow to the branch, often reaching the trunk of young trees where it may girdle and kill the tree. All four North American white pines (*P. monticola*, *P. flexilis*, and *P. albicaulis* in the west and *P. strobus* in the east) are classed as susceptible to very susceptible, whereas many Eurasian and a few other North American white pines are considered immune or resistant (Bingham, 1983). The susceptibility of whitebark pine to the rust coupled with the threat from the mountain pine beetle (*Dendroctonus ponderosae*) and catastrophic fire may cause the species to soon be listed under the Endangered Species Act

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Fig. 1. Whitebark pine tree in foreground near the timberline on Mt Rainer in Washington State.

(Mahalovich and Dickerson, 2004). It has not yet been placed there but is classed as vulnerable (Farjon, 1998).

In 2001, a program was initiated in Idaho, Montana, Nevada, Wyoming and eastern Washington to designate permanent trees to be left that appear rust resistant and plus trees were selected to be screened for rust resistance and serve as a seed source for operational collections of cones for seed extraction and use in regeneration. Survivors of blister rust screenings are to be placed in clone banks for gene conservation and will serve as donors of scion for future seed orchard establishment (Mahalovich and Dickerson, 2004). There are several unanswered questions regarding the cone and seed potential of such trees and the possible reproductive constraints to seed production from wild trees and ramets when placed in seed orchards. The purpose of this study was to do cone and seed analyses to determine the seed potential of whitebark pine cones collected from two natural stands and determine the types of seeds produced and, based upon developmental literature, determine the probable causes for the loss of viable filled seeds.

2. Materials and methods

Cones were collected from trees at two sites: (1) Mt Rose at 17N, 18E Sections 24, 25, and 30 (39.3136 latitude and 119.9388 longitude) in Nevada at elevations between 2618 and 2784 m; and (2) Brundage at 19N, 03E in Section 7 (44.9988 latitude and 116.137 longitude) in Idaho at an elevation of 2195 m in late September 2004. Five cones were collected from each of seven trees at Mt Rose and five cones were collected from each of two trees at Brundage. The five cones from each tree were placed in a canvas bag and the bag was tied and labeled. All cones were placed in cold storage over-winter. By spring the collected cones were dry and still intact (Fig. 3) but they crumbled easily without further drying or treatment. Each cone was weighed, the length measured and the total number of scales counted. Each cone was then pulled apart by hand from bottom to top and the numbers of sterile scales (lacking any seeds) at the bottom and top of the cone were counted and subtracted from the total scales to determine the number of fertile scales in the cone. There were no sterile scales in the middle 80–90% of the cone. All seeds were removed from the scales and axis of each cone. For each cone the total seeds were counted and seeds were placed in water for a few minutes to soften the seed coat. They were then stuck onto masking tape and each seed was sliced longitudinally with a razor blade and the contents examined using a dissecting microscope. Eight categories of seeds (Table 1) were recognized: (1) filled seeds had a normal megagametophyte that filled the seed and contained a well-developed embryo (Fig. 6). These were considered to be viable; (2) small flat ovules that had aborted before pollination (Fig. 9); (3) small rounded ovules that had aborted soon after pollination (Figs. 10 and 11); (4) fully enlarged seeds in which the megagametophyte and embryos had aborted and dried at about the time of fertilization (Fig. 12); (5) fully enlarged seeds that contained a collapsed mega-gametophyte and small collapsed mid-embryo (Fig. 13); (6) fully enlarged seeds that contained a partially collapsed megagametophyte and an aborted late embryo (Fig. 14); and (7)
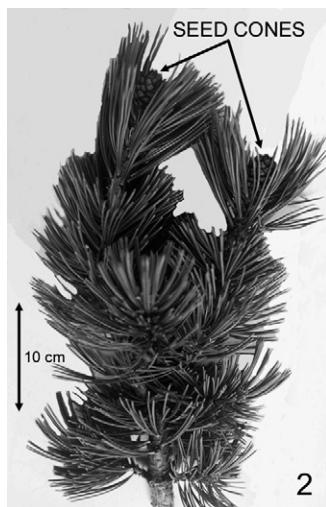

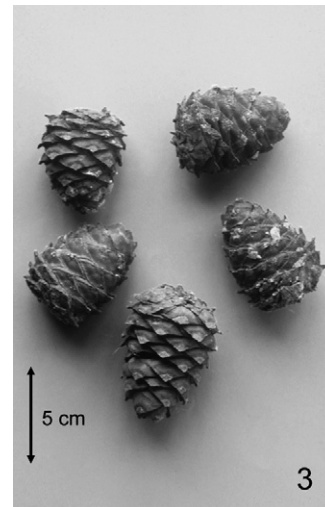Fig. 2. Branch collected in mid-summer showing 2nd year seed cones.

Fig. 3. Mature seed cones.

Table 1
Whitebark pine cone and seed analyses for two high-elevation sites in the Inland Empire in 2004

Site	Cone length (cm)	Cone weight (gm)	Total scales	Sterile scales top	Sterile scales bottom	Fertile scales	Percent fertile scales	Seed potential	Total seeds	Filled seeds	Aborted seeds not pollinated	Aborted seeds at pollination	Aborted seeds at fertilization "Empty"	Aborted seeds at early embryo	Aborted seeds at late embryo	Insect-/disease-damaged seeds	Seed efficiency (% filled)
1 (35)	6.1	24.2	59	4.2	17	46	77.5	92	76.7	49.5	0.2	2.3	13.5	7.6	2.2	1.3	64.5
2 (10)	7	34.6	73	5.8	10.8	55	74.8	110	94.6	42	0	18.2	26.3	5.7	0.1	2.3	44.4
Avg	6.3	26.5	62	4.5	15.6	48	76.9	96	80.5	47.8	0.2	5.8	16.3	7.2	1.7	1.5	59.3

Site-1 had 7 trees and a total of 35 cones and Site-2 had 2 trees and a total of 10 cones. Numbers shown are averages for each site.

insect-damaged or diseased seeds (Figs. 15–17). From this information the percentage of fertile scales and the seed efficiency (SEF = filled seeds/total seeds) were calculated (see Table 1). The causes for the different categories of seeds were determined from the literature on seed development that is available for pines and other conifers over the last 50 years and is reviewed by Dogra (1967) and Owens et al. (2005).

3. Results and discussion

The cones were borne laterally near the tips of branches. They were pollinated in the spring, became dormant during the summer and over-wintered as small cones 2–3 cm long. The cones resumed growth the following spring, became 3–4 cm long at fertilization in late June or July of the 2nd year (Fig. 2) and matured by fall. In the fall, shoots may bear dormant 1st-year cones near the tip of the shoot and more proximal mature 2-year old cones. This position of cones indicates that whitebark pine has a typical pine life cycle, with 1 year between pollination and fertilization and cones maturing in the 2nd year.

The seeds of whitebark pine lack seed wings so wind dispersal is not efficient. Mature cones may be shed and decay releasing seeds. More commonly in natural stands, seed dispersal is aided by birds that collect seeds form mature cones on the tree and store them in groups in the rocky ground nearby. The interesting ecological relationship between Clark's nutcracker (*Nucifraga columbiana*), native to areas of white-bark pine distribution, has been described in detail by Lanner (1982). Mature cones are also collected by small mammals and stored. Both methods are important in seed dispersal for wingless seeds in a species with a very scattered distribution. Birds may reduce the number of filled seeds in cones before they are collected and small mammals may reduce the number of available cones that may be collected.

In the present study, mature cones that were harvested were dark green to brown and became browner with storage. Mature cones averaged 6.3 cm in length (range 5–8 cm) and averaged 24 g (range 15–36 g) at the Mt Rose site and 7 cm in length (range 6–8 cm) and 35 g in weight (range 19–47 g) at the Brundage site. The average number of total scales for the two sites was 62. The smaller cones from the Mt Rose site averaged 59 total scales and those at the Brundage site 73 total scales. There were a few sterile scales at the tip of the cone (average 4.5) and more sterile scales at the base of the cone (average 15.6) at both sites. The average number of fertile scales was 46 giving a seed potential of 92 seeds per cone at the Mt Rose site.

The larger cones from the Brundage site averaged 10 more fertile scales and a seed potential of 110 seeds per cone (Table 1).

The total seeds extracted per cone, including all categories of seeds, were 63 at Mt Rose and 68 per cone at Brundage. The numbers of filled seeds per cone averaged 50 at Mt Rose compared to 42 per cone at Brundage. This resulted in seed efficiency about 12% higher with a higher number of filled seed per cone at the Mt Rose site, even though the cones were generally smaller cones with fewer fertile scales than at the Brundage site.

Different categories of seeds and the loss of filled seeds result from different causes acting at different times during the 15–16 months reproductive cycle, from pollination to cone maturity. The possible causes for the various types of seeds were determined from earlier studies of cone, seed and embryo development in other conifers (Dogra, 1967; Owens et al., 1990, 1991, 1994; Owens, 1993; Owens and Morris, 1998; Anderson et al., 2002) including pines (Owens and Molder, 1997b; Owens et al., 1982, 2005; Owens, 1993; Owens and Fernando, 2007).

Filled whitebark pine seeds are 8–10 mm long, the upper (adaxial) seed surface is dark brown, smooth and mottled (Fig. 4) and the lower (abaxial) surface that was attached to the scale is light brown and rough (Fig. 5). No seed wing develops from the ovuliferous scale or the ovule. The seed coat is thick but slices easily with a razor blade if the seeds are soaked in water for a few minutes. Soaking for a short time softens the seed coat but does not hydrate the megagametophyte or embryo. It is more difficult to observe and interpret the condition of hydrated seeds. In the sliced seeds the seed coat is thick with a thin outer and inner brown sarcotesta and endotesta, respectively, and a thick cream-colored sclerotesta between (Fig. 6). The megagametophyte nearly fills the seed
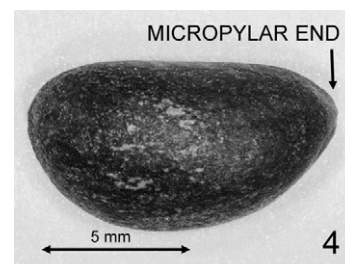

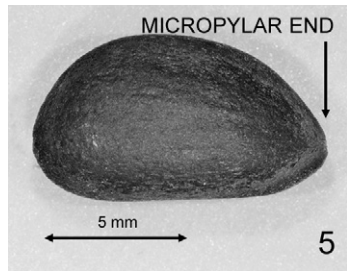Fig. 4. Upper (adaxial) surface of wingless seed that is dark brown and has a mottled surface.

Fig. 5. Lower (abaxial) surface of a seed that was loosely attached to the scale is light brown and smooth.

Fig. 8. Filled healthy seed with seed coat and megaspore wall removed to show the yellow megagametophyte and the dried nucellus (nucellar cap) at the micropylar end.

cavity in non-hydrated seeds (Fig. 6) and is enclosed by a thin brown megaspore membrane (Figs. 6 and 7). The sliced megagametophyte in healthy seeds is white and the embryo fills about 80% of the length of the megagametophyte (Fig. 6). There is a narrow corrosion cavity around the embryo. The distal 20% and proximal 20% of the embryo consist of cotyledons and suspensor, respectively. The root apex occupies another 20% of the embryo and the hypototyl-shoot axis the remaining 40% (Fig. 6). Remnants of the nucellus form a brown nucellus tip at the micropylar end of the megagametophyte. This is visible if the megaspore membrane is removed (Fig. 8).

Sterile scales on which no ovules develop bear no seeds. These occur at the base and tip of the cones and may occasionally occur in the mid-region of whitebark pine cones. In western white pine that has been studied in detail (Owens and Molder, 1977a; Owens, 2004; Owens and Fernando, 2007) seed cones develop and form ovuliferous scales and ovules in the spring, just before pollination. These ovules, if they were pollinated and fertilized, develop into mature seeds about 15 months later (Owens and Molder, 1997b; Owens, 2004). Some ovules do not develop enough to be pollinated by the time

pollination has ended. These ovules abort leaving very small flattened ovules, "seeds" at the base of the scale (Fig. 9). These account for less than 1% of the seed potential in whitebark pine (Table 1). Most ovules develop enough to have a well-developed pollination mechanism but they may not be pollinated. Ovules that are not pollinated abort soon after the time of pollination and remain as small seeds in the mature cone. Other ovules may be pollinated but abort at or soon after pollination. Non-pollinated ovules and ovules that abort at or soon after pollination look the same externally (Fig. 10) and when sliced (Fig. 11). They have a thick seed coat but the megagametophyte within is small and brown. They develop no further and remain as small rudimentary seeds (Figs. 10 and 11). These represented about 6% of the seed potential in the whitebark pine cones (Table 1).

The greatest loss of filled seed resulted from the formation of partially filled but inviable seeds. These seeds may have aborted during megagametophyte development not long before fertilization, at the time of fertilization or during embryo development following fertilization. Some authors combine all of these aborted seeds into one category and call them "empty" seeds but they are not empty. They contain dried brown material that is the dead remains of the completely aborted mega-
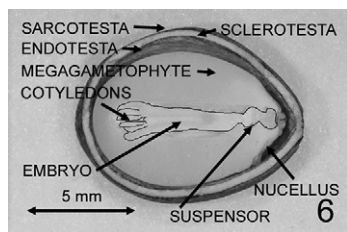

Fig. 6. Filled healthy seed sliced open to show the thick seed coat, consisting of an outer (sarcotesta), middle (sclerotesta) and inner (endotesta). The white megagametophyte contains a cream to yellow well-developed embryo (outlined). The nucellus covers the micropylar end of the megagametophyte.
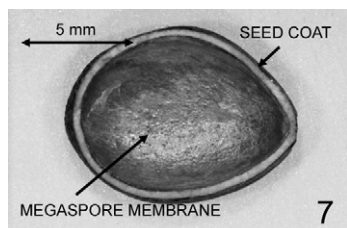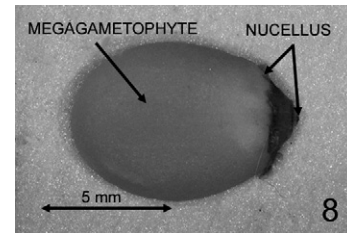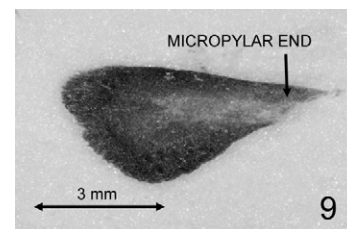

Fig. 9. A flat ovule that aborted before pollination and contains no megagametophyte.

Fig. 7. Filled healthy seed with the top half of the seed coat sliced off to show the surface of the light brown megaspore wall (membrane).
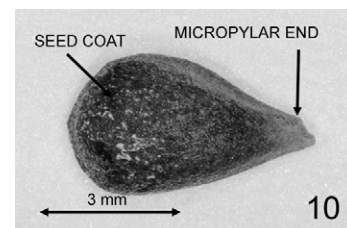

Fig. 10. Upper (adaxial) surface of a small rudimentary seed that was not pollinated and aborted or aborted soon after being pollinated.
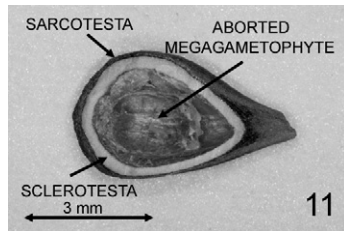
Fig. 11. Sliced rudimentary seed showing thick seed coat and aborted megagametophyte within.

Fig. 13. Sliced seed that aborted during early embryo development.

Fig. 14. Sliced seed that aborted mid-way through embryo development. Megagametophyte is white, small and irregular.

gametophyte or some white material that is the remains of a partially aborted megagametophyte or embryo. The nature of the contents indicates when the seed aborted and the possible cause of the abortion. During the pre-fertilization 2nd year development, the megagametophyte changes from a fluid-filled sac with a peripheral layer of nuclei or cells into a sac filled with about 2000 parenchyma cells containing large fluid-filled vacuoles. Megagametophyte cells remain at this stage of development during fertilization and early embryo development, until about 2 weeks after fertilization. Megagametophytes that abort during this time degenerate and dry forming a brown collapsed sac (Fig. 12). After fertilization the parenchyma cells of the megagametophyte begin to accumulate lipid and protein bodies that soon nearly fill the cells during mid- to late-embryo development (Owens et al., 1993). The more lipid and protein that is present, the less the megagametophyte will collapse if it aborts, therefore seeds aborting during mid- to late-embryo development retain some white megagametophyte or embryo tissues (Figs. 13 and 14). During the last stages of seed development all lipids and proteins have been stored and the megagametophyte and embryo dehydrate. Abortion at this time causes little collapse of the megagametophyte but it usually becomes discolored as does the remains of the aborted embryo.

The largest category of aborted seeds was those that aborted at the mature megagametophyte stage. About 13 and 26 seeds per cone aborted at this stage at Mt Rose and Brundage,

respectively, for an average of 20 seeds per cone, about 20% of seed potential (Fig. 12). About seven seeds per cone aborted at the early embryo stages (Fig. 13) and only about one seed per cone at the late-embryo stages (Fig. 14) (Table 1). Seeds aborting at these times externally look normal in size, shape and color (Figs. 4 and 5) because the seed coat is well developed by the time of fertilization.

Insect-damaged seeds are usually full size with a well-developed seed coat but there is often an exit-pore through the seed coat, commonly at the micropylar end (Fig. 15). Sliced seeds show the remains of the megagametophyte that may be white or brown (Fig. 15) containing a cavity in which the larva lived and fed (Figs. 15 and 16). A few seeds appeared to be insect- or disease-damaged and contained a deformed white megagametophyte (Fig. 17). Only about 2% of the mature seeds were insect- or disease- damaged but several of the cones were totally destroyed by insects and could not be analyzed. If a cone was insect-damaged it tended to have nearly or all of the seeds destroyed. These cones were more common at the Brundage site and the damage was obvious from viewing the surface of the cone. These cones often become case-hardened and should not be collected. Cones with no visible external damage usually had few insect-damaged seeds and should be collected.

In laboratory and field studies of the entomofauna of whitebark pine it was determined that mature and immature
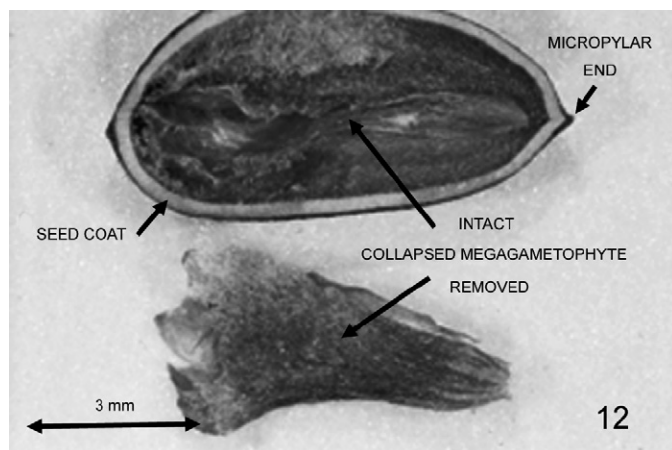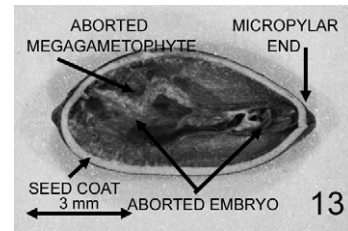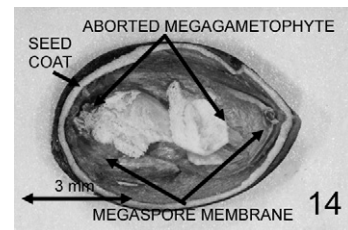

Fig. 12. Sliced "empty seed" (upper) showing the collapsed brown sack-like megagametophyte that aborted about the time of fertilization, about 1 year after pollination and (lower) a collapsed megagametophyte that has been removed from an "empty seed".
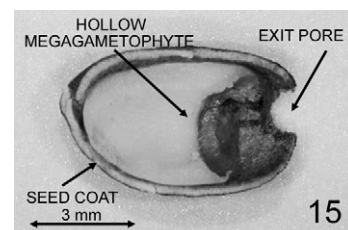

Fig. 15. Sliced insect-damaged seed showing large insect exit-pore and damaged white megagametophyte.
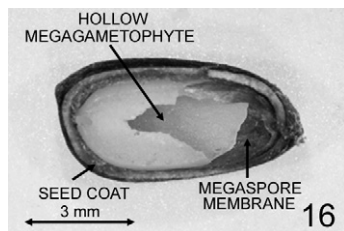
Fig. 16. Sliced insect-damaged seed containing a white, thin, hollow mega-gametophyte.
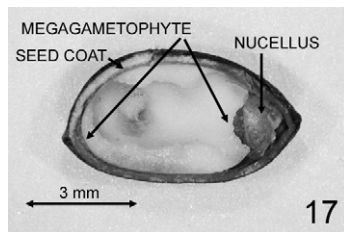

Fig. 17. Sliced seed showing a frothy white megagametophyte that resulted from unknown causes.

Leptoglossus occidentalis (the western conifer seed bug) can use cones and foliage of whitebark pine as a food source for short periods of time (Anderton and Jenkins, 2001). But it was not determined if this insect occurred naturally at the five high-elevation sites at which the study trees were growing. Larvae of several unidentified Lepidoptera species were found in the cones at some sites but these never damaged more than 5% of the seeds. Cecidomyiid (Diptera or fly) larvae were found between cone scales of cones from most sites and larval *Megastigmus* sp. (seed chalcids) were in 4.7% of the X-rayed seeds. Several other insects were found on cones but it was not determined if they caused cone or seed damage. Clearly, there is the possibility of considerable insect-damage to whitebark pine seeds and cones in nature and in seed orchards.

When evaluating cone crop quality for operational collections, recommendations for the minimum number of filled seeds exposed on one-half cone face are typically provided (Portlock, 1996). No guidelines currently exist for whitebark pine (Eremko et al., 1989). Based on the limited samples examined, a preliminary recommendation of 10 filled seeds per half cut-face should be sought before expending resources to collect cones from whitebark pine. Based on the filled seeds per cone at the two sites, for every 1000 filled seeds, about 20 cones (0.5 kg of cones) would be needed from the Mt Rose site which had smaller cones and about 23 cones (0.8 kg of cones) would be needed from the Brundage site which had the larger cones. It should be remembered that larger cones do not necessarily produce more viable seeds. In general, for both sites, it would be safe to assume that each kilogram of cones may yield about 2000 filled and viable seeds.

4. Summary

It is possible to determine seed potential, the number of filled seeds and the causes for the loss of filled seeds during cone development based on cone and seed analyses of mature cones if the reproductive biology of the genus is known. This was possible for whitebark pine as it was for lodgepole pine (Owens et al., 2005) and western white pine (Owens and Fernando, 2007). In whitebark pine from two high-elevation sites, cones had a typical 2-year pine reproductive cycle, with pollination occurring in the spring of 2003, fertilization in June or July of 2004 and cones maturing in the fall of 2004. Cones had an average of 62 scales, about 75% of which were fertile giving an average seed potential of 96 seeds per cone. The total seeds extracted per cone was 66 per cone of which 46 (70%) were filled. Seeds were lost (aborted) due to several different causes: (1) less than one seed per cone was lost because the ovule aborted before pollination; (2) about 10 seeds per cone were lost because ovules aborted soon after pollination either due to a lack of pollination or early incompatibility mechanisms; (3) 20 seeds per cone were lost about the time of fertilization, likely due to self-incompatibility resulting in the collapse and drying of the megagametophyte; (4) another eight seeds per cone were lost due to embryo abortion at the early to late-embryo stages; and (5) about two seeds per cone were lost due to insects or disease. Some cones were badly damaged by insects and contained no filled seeds, and thus could not be accurately analyzed. The seed efficiency per cone, determined as the percent of the total seeds in the five categories above that were filled and likely viable, was 70%. This is high-seed efficiency and filled seeds per cone for a high-elevation conifer species and indicates that whitebark pine was a good seed producer in these two natural stands in 2004. It also suggests that whitebark pine could be a good seed producer in lower elevation seed orchards if good cone production can be obtained, pollen production and pollination are satisfactory and insect and disease problems are controlled. At least 10 filled seeds per half cut-face should be sought before expending resources to collect cones from whitebark pine.

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